

THE CALIFORNIA ISLANDS¹

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ABSTRACT

The California Islands off the Pacific coast of southern and Baja California display almost diagrammatically the insular phenomena that characterize fringing archipelagos. To a lesser extent they also illustrate some of the insular features associated with oceanic islands. Several of these islands have been much studied and are relatively accessible.

The location, size, elevation, and geological history of the islands are described. To determine the degree of disharmony of the island floras, they are analyzed in comparison with selected California mainland floras. The degree of richness of the island floras is discussed in relation to size of the islands, proximity to the mainland, and other variables.

Such phenomena of island life as the immigrant pattern of vertebrate distribution, relict *versus* autochthonous endemism of plants and animals, insular gigantism, continuous flowering, high degree of hybridization, vulnerability, and loss of dispersibility in island species are considered in reference to the California Islands. Some suggestions as to available facilities on the islands and persons or institutions to contact are given in an epilogue.

Off the Pacific coast of southern California and Baja California, Mexico, lie the islands variously called the Channel Islands or California Offshore Islands and the Baja California Islands or, collectively, the California Islands. Although they are in no sense tropical, they are worthy of mention in this symposium because they are a good example of a fringing archipelago and because they illustrate many of the insular phenomena that one might otherwise have to travel far to tropical areas to study. Some of them are quite accessible from the heavily populated areas of southern California, and some of them have been rather thoroughly studied by biologists. Although they are, thus, rather well known to California biologists, they are surprisingly little known to non-Californians. It is hoped that this short discussion of them and of some of their insular characteristics will create more interest in them among those biologists concerned with evolutionary and environmental phenomena.

The Southern California and Baja California Islands consist of 16 major islands or island groups spread over some 500 miles between Point Conception, California, and Punta Eugenia, Baja California, Mexico (Fig. 1). From east to west the Northern Channel Islands are Anacapa, Santa Cruz, Santa Rosa, and San Miguel. The Southern Channel Islands are San Nicolas, Santa Barbara, Santa Catalina, and San Clemente Islands. The Baja California Islands include Los Coronados just south of San Diego, Todos Santos off Ensenada, San Martin off San Quintin, San Gerónimo south of El Rosario, the San Benitos, Cedros, and Natividad off Punta Eugenia, and Guadalupe 157 miles off the Baja California peninsula.

In order of size, with area in square miles, the islands are: Cedros (134), Guadalupe (98), Santa Cruz (96), Santa Rosa (84), Santa Catalina (75), San

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Clemente (56), San Nicolas (22), San Miguel (14), Natividad (2.8), San Benito (2.5), Anacapa (1.1), Santa Barbara (1.0), Los Coronados (1.0), San Martin (0.9), Todos Santos (0.5), and San Gerónimo (0.2). Their distances from the mainland, in statute miles, are: San Martin (3), Todos Santos (4), Natividad (5), San Gerónimo (6), Los Coronados (8), Anacapa (13), Cedros (14), Santa Cruz (19), Santa Catalina (20), San Miguel (26), Santa Rosa (27), Santa Barbara (38), San Benito (41), San Clemente (49), San Nicolas (61), and Guadalupe (157). All these figures are from a summary by Philbrick (1967). The highest elevations on the largest islands, in feet, are: Guadalupe (4,257), Cedros (3,950), Santa Cruz (2,165), Santa Catalina (2,069), San Clemente (1,965), Santa Rosa (1,574), and San Nicolas (907).

GEOLOGICAL HISTORY

Also most pertinent to an understanding of the biology of these islands is the probable geological history of the islands and their biota. The following geological information was gleaned from various sources, but especially from Axelrod (1967*b*), Orr (1967), Reed (1933), Smith (1933), Valentine and Lipps (1967), and Weaver and Doerner (1967).

The islands appear to have had rather diverse origins. All of them, except Guadalupe, are probably of continental origin, for they appear to be the emergent tops of elongated mountain ridges separated by deep submarine basins on the broad continental borderland. The four Northern Channel Islands, an east-west chain, are disjunct segments of the Santa Monica Mountains, or Anacapia, on the south edge of the California Transverse Ranges. They have had an active history of emergence and submergence. Western Anacapia may have formed the northern edge of the larger ancient land mass known as Catalinia, which included the present Southern Channel Islands and the Palos Verdes Hills, a former island now joined to the mainland. Catalinia probably appeared in Cretaceous time. It underwent intermittent periods of uplift and submergence, and it may occasionally have been connected with the mainland. It unloaded great quantities of sediments into a seaway to the east during Miocene time, and its basin and range topography is due to block-faulting, which probably dates in part from the Miocene.

Anacapia may have had a pre-Cenozoic origin as reflected in its granitic core intruded into metamorphic rocks that are overlain by Cretaceous and pre-Pliocene sedimentary and volcanic rocks, which in turn are capped by Pleistocene terrace formations. Apparently Anacapia was joined to the mainland in Oligocene, Miocene, Pliocene, and late Pleistocene times, but these emergences were separated by submergences, particularly in Miocene and Pleistocene times, that may have nearly or completely destroyed terrestrial biotas. Thus, the present biota of the Northern Channel Islands may largely date from pre-Illinoian time in the Pleistocene when the northern islands were connected to the mainland as an east-west trending peninsula. Previous to this time, as suggested by wave-cut platforms on the top of Farrel Mountain on Santa Rosa, to near the top of Green Mountain on San Miguel, and to 1,800 feet on the north side of Santa Cruz, only the highest peaks of one

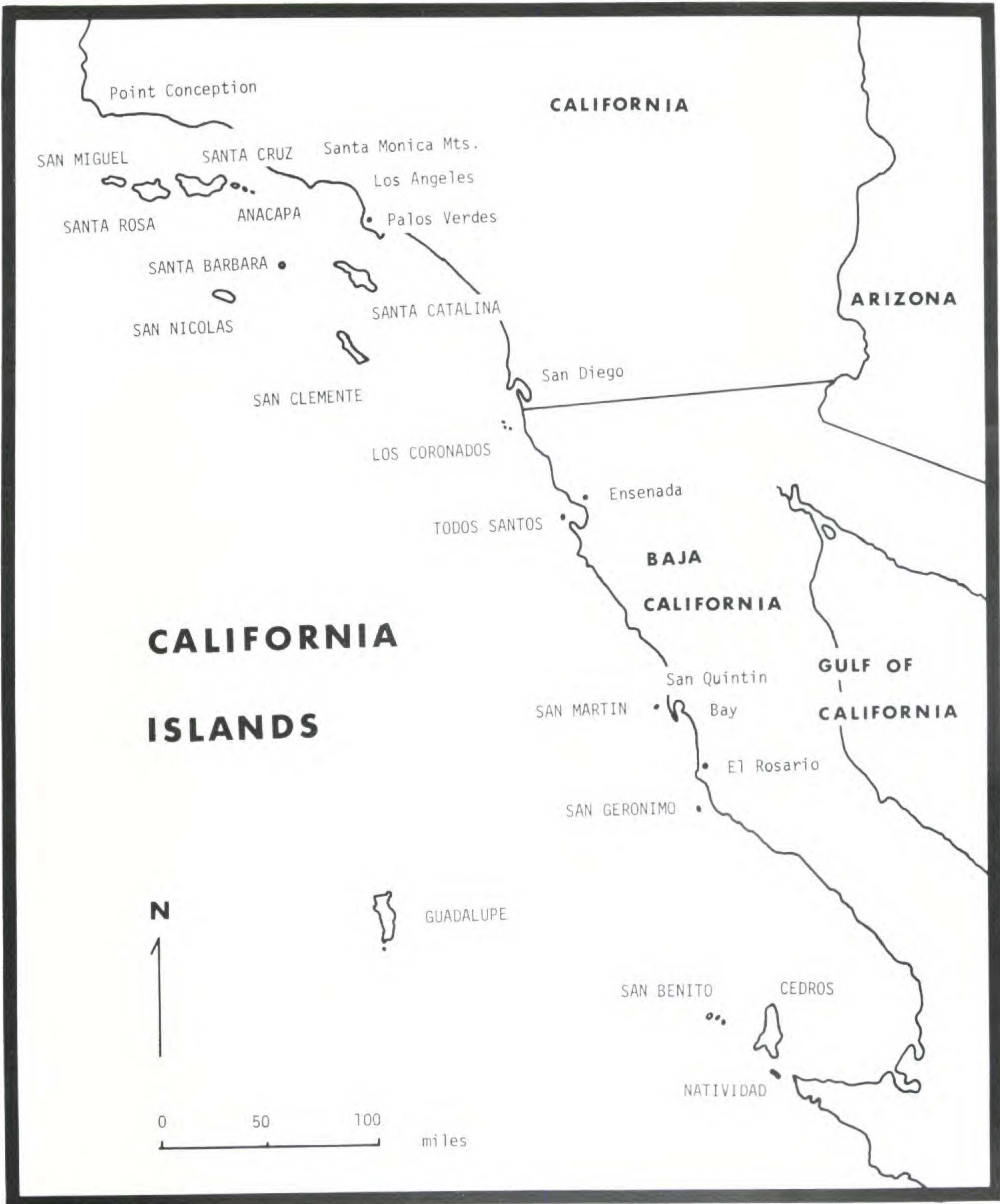


FIGURE 1.—Outline map of the California Islands.

island, Santa Cruz, may have been above water. Fossil remains of dwarf mammoths in Pleistocene terrace deposits on Santa Cruz, Santa Rosa, San Miguel, and San Nicolas Islands (D. E. Savage & Downs, 1954) surely require terrestrial connections of these islands with each other and with the mainland through the Anacapas during the Pleistocene, perhaps a half million years ago. By Illinoian time the northern islands were cut off from the mainland. There is evidence that aboriginal man butchered and cooked a dwarf mammoth on Santa Rosa some 27,000 years ago (Orr, 1967). During the Iowan or lower Wisconsin glacial stages from about 11,000 to 20,000 years ago, lowered sea levels permitted

the connection of the Northern Channel Islands with each other but not with the mainland.

The geological history of the Southern Channel Islands is somewhat different. It is likely that the biotas of all of them have arrived over water. San Nicolas lies on a shallow submarine ridge running southeast from Santa Rosa and may have been connected to it terrestrially in the Pleistocene, as suggested by the fossil remains of the dwarf mammoth on San Nicolas. However, marine terrace deposits covering much of the central and northwestern portions of the island indicate total submergence in the late Pleistocene (Foreman, 1967). The much smaller and lower Santa Barbara Island was presumably also completely submerged at that time. Surf-cut terrace platforms, from sea level to nearly 2,000 feet, are also conspicuous on San Clemente, Santa Catalina, and the Palos Verdes Hills. On most of the islands they bear fossiliferous marine sediments. Radiometric age estimates suggest that the terraces on the Palos Verdes Hills range in age from about 380,000 to 120,000 years before the present. The higher terraces on the islands may be considerably older, even early Pleistocene in age. The nearly 20 distinct wave-cut terraces extending to 1,500 feet on San Clemente and the rather flat plateau-like summit area (highest elevation 1,965 feet at Thirst) would seem to leave little, if any, of that island above water at its greatest submergence. Similarly, the marine terraces to about 1,700 feet on Santa Catalina, the nearly horizontal line of the main ridge at about 1,550 feet, and the rounded summit elevations suggest prolonged marine abrasion during Pleistocene time. Little if any of the island could have remained above water from the Pliocene emergence. This submergence, along with the great depth of the San Pedro Channel separating Santa Catalina from the Palos Verdes Hills, precludes migration overland to the island during the Pleistocene.

Of all the California Islands, only Guadalupe is clearly oceanic. Volcanic in origin, it rises some 15,000 feet from the sea bed, 157 miles from the peninsula of Baja California. Depths of some 12,000 feet lie between the island and the peninsula. The oldest lava flow on the island is reported to be about 7 million years old (Hubbs, 1967). One can hardly question the over-water origin of its biota. The other Baja California Islands, except the San Benitos, are within a few miles of the coast of Baja California, and probably were connected to the peninsula during the lowest sea level of the Wisconsin glacial stage, perhaps 20,000 years ago. Little attention will be given to these onshore islands in the following discussion.

DISHARMONIC ISLAND BIOTAS

Disharmony of insular biotas has been discussed by many students of island life, most recently by Thorne (1963, 1965), Carlquist (1965), and Balgooy (1969). An island that is a recently separated continental fragment may be expected to have a biota nearly as balanced, rich, diverse, and representative as that of an area of comparable size and diversity of habitat on the adjacent continent. An isolated oceanic island, on the contrary, may be expected to have a depauperate, disharmonic biota lacking numerous groups of organisms ill-adapted to long-

distance dispersal over water. Numerous ecological niches on such islands remain empty or are filled by organisms not normally found in similar continental niches. Comparison of the biota of an island with that of a similar area of the adjacent mainland should suggest whether the insular biota came over water or remains from a former continental connection. A quick examination of the present biotas of the California Islands, at least the offshore islands, suggests that they are mostly depauperate aggregations of plants and animals that have reached the islands by chance over-water dispersal. The floras of Santa Cruz and Santa Rosa Islands include remnants of a once richer continental flora. This last conclusion is supported by the late Pleistocene Willow Creek flora of Santa Cruz Island, which included such woody plants as *Pseudotsuga* Carr., *Cupressus goveniana* Gord., *Ceanothus thyrsiflorus* Esch., *Cornus californica* C. A. Mey., *Garrya elliptica* Dougl., and *Myrica californica* Cham. & Schlecht. (Axelrod, 1967*b*), all now vanished from the present insular flora.

The area of mainland southern California most nearly similar in size and topography to the Northern Channel Islands and Santa Catalina is the Santa Monica Mountains, or Eastern Anacapia, which is separated from Western Anacapia by the Santa Barbara Channel. Table 1 compares the flora of these mountains with floras of other California mainland areas, mostly along the moister central coast, and of various of the better known California Islands. The data for

TABLE 1. Statistical summary of indigenous taxa in selected California floras.

	Area in Square Miles	Families	Genera	Species, Sub- species, Vari- eties & Hybrids
A. MAINLAND AREAS				
1. Monterey County	3,324	105	433	1,422
2. Santa Cruz Mountains (San Francisco and Santa Cruz Counties)	1,386	108	445	1,246
3. Marin County	529	106	410	1,010
4. Santa Monica Mountains (Los Angeles and Ventura Counties, in part)	320	93	312	640
5. Santa Rosa Plateau (Riverside County, in part)	70	82	241	409
6. San Francisco County	45	91	304	661
7. San Bruno Mountains (San Francisco and San Mateo Counties, in part)	4.7	69	228	384
B. CALIFORNIA ISLANDS				
1. Cedros	134	56	173	205
2. Guadalupe	98	51	127	167
3. Santa Cruz	96	70	237	420
4. Santa Rosa	84	65	212	340
5. Santa Catalina	75	75	237	407
6. San Clemente	56	54	166	239
7. San Nicolas	22	32	71	106
8. San Miguel	14	39	110	190
9. Santa Barbara	1	26	54	65

the table were gleaned from the following sources: for Monterey County, Howitt and Howell (1964); Santa Cruz Mountains, Thomas (1961); Marin County, J. T. Howell (1949); Santa Monica Mountains, Raven and Thompson (1966); Santa Rosa Plateau, Lathrop and Thorne (1968) and Thorne and Lathrop (1969); San Francisco County, J. T. Howell, Raven, and Rubtzoff (1958); San Bruno Mountains, McClintock and Knight (1968); California Islands in general, Eastwood (1941) and Raven (1967); Cedros Island, Moran (1967; personal communication, 1970); Guadalupe Island, Eastwood (1929), J. T. Howell (1942) and Moran (1951, 1967, 1969; personal communication, 1970); Santa Catalina Island, Thorne (1967, 1969); San Clemente Island, Raven (1963) and Thorne (1969); San Nicolas Island, Foreman (1967); and Santa Barbara Island, Dunkle (1950) and Philbrick (1969).

Among the harmonic mainland floras there is an expected decrease in richness of flora with decrease in area at least with reference to the maritime floras of central California. The two southern California floras, for the Santa Monica Mountains and Santa Rosa Plateau, are considerably less rich for their size, presumably because of more arid climate and less ecological diversity. Among the insular floras, those of the larger islands closest to the mainland, Santa Cruz, Santa Rosa, and Santa Catalina, are relatively harmonic. Santa Cruz and Santa Rosa Islands have relatively rich floras and a larger number of tree and shrub species than Santa Catalina or San Clemente Islands. Among the more significant of these woody plants are: *Pinus muricata* D. Don (including *P. remorata* Mason), *P. torreyana* Parry ex Carr., *Acer macrophyllum* Pursh, *Arbutus menziesii* Pursh, four species of *Arctostaphylos* Adans., *Berberis (Mahonia) pinnata* subsp. *insularis* Munz, an undescribed *Garrya*, *Pickeringia montana* Nutt., many species of *Quercus*, including *Q. agrifolia* Neé, *Q. wizlizenii* var. *frutescens* Engelm., *Q. douglasii* H. & A., *Ribes malvaceum* Sm., *R. thacherianum* (Jeps.) Munz, and *Vaccinium ovatum* Pursh. These plants reflect moister conditions on the Northern Channel Islands and perhaps also suggest the retention of some species from the period of Pleistocene connection with the mainland.

The relatively harmonic flora of Santa Catalina more likely results from its close proximity to the mainland, only 20 miles off the Palos Verdes Hills, rather than from any former terrestrial connections, which geologically appear most unlikely since the early Pleistocene rise of the island. It lacks all the woody species listed above for Santa Cruz and Santa Rosa Islands.

The floras of the outer islands, such as San Clemente, San Nicolas, Santa Barbara, and San Miguel, are clearly depauperate and unbalanced. However, most disharmonic of all is the flora of the isolated volcanic oceanic island of Guadalupe despite its great age and relatively large size and high elevation. It presumably had a very depauperate flora even before its present devastation by goats. The relatively poor flora of the onshore Isla de Cedros is probably due to the rather arid climate of the island and of the adjacent mainland.

Various attempts have been made to correlate richness of flora with size of island. Too many variables, however, make such efforts rather futile. An analysis of the California Islands shows that in addition to size, other, often more im-

portant, factors are zonal climate, proximity to the mainland or to other large high islands nearer the mainland, elevation and topographic diversity, ecological diversity (as affected by topographic diversity, elevation, precipitation, and soil types) of the island and the adjacent continent, age of the island, and direction of currents, winds, and storms in conjunction with direction of the island from the continent or nearest high islands.

IMMIGRANT PATTERN OF DISTRIBUTION

As explained rather thoroughly by Darlington (1957), a fringing archipelago receives its vertebrate animals from the adjacent continent in approximate proportion to their vagility, *i.e.*, their dispersibility, and in an orderly way along the probable routes of immigration into the islands. Birds and bats are relatively numerous and little if at all differentiated from mainland populations. Lizards are well represented among the herpetofauna. Amphibians and terrestrial mammals, mostly small, are poorly represented. Most of the relictual endemic vertebrates will be on the islands closest to the mainland, except in the more vagile groups, wherein the relicts tend to be on islands farthest from the mainland.

In regard to these characteristics, as well as to others, the California Islands fit well Darlington's definition of a fringing archipelago. Birds and bats, and the marine pinnipeds (seals and sea lions), are very well represented and are seldom recognizably distinct from the mainland populations. Of 15 non-marine mammals known to be indigenous on the California Islands (Bloeker, 1967), nine species are bats. The other six are a depauperate assemblage of small mammals that must have reached the islands over water as waifs. Of the depauperate herpetofauna of 28 reptiles and amphibians (J. M. Savage, 1967), all but four are found also on the mainland, mostly adjacent to the islands. The 13 lizards are relatively well scattered over the more accessible California Islands, but only two have reached the more isolated San Nicolas and San Clemente and only one the small isolated Santa Barbara Island. The eleven snakes are restricted to Santa Cruz, Santa Catalina, and the onshore islands of Baja California. The four amphibians, one frog and three salamanders, are known only from the Northern Channel Islands, Santa Catalina, Los Coronados, and Todos Santos Islands. No indigenous reptiles, amphibians, or mammals are reported from the oceanic island of Guadalupe, which, however, did formerly have eight endemic species or subspecies of birds (Moran & Lindsay, 1950). The distribution of the few vertebrate relicts will be discussed below.

RELICT ENDEMISM

The outstanding feature of the California Islands is their high percentage of relict endemics. As a fringing archipelago they should be rich in endemics that have been eliminated from mainland habitats. Autochthonous endemics, on the other hand, should be relatively few and poorly marked. This is indeed the case. No family of plants is endemic to the California Islands though one of the two species of Crossosomataceae, *Crossosoma californicum* Nutt., is restricted to Santa

Catalina, San Clemente, and Guadalupe Islands. Four monotypic genera are endemic to the islands, *Hesperelaea* A. Gray (Oleaceae) and *Baeriopsis* Howell (Asteraceae) on Guadalupe, *Munzothamnus* Raven (Asteraceae) on San Clemente, and *Lyonothamnus* A. Gray (Rosaceae) on the larger Channel Islands. The *Hesperelaea* is now apparently extinct. Considering only Guadalupe and the Channel Islands there are 119 species and subspecies (or equivalent varieties) of seed plants restricted to the islands, with 32 of these endemic to Guadalupe Island. Thirteen are restricted to San Clemente, nine to Santa Cruz, seven to Santa Catalina, five to Santa Rosa, and two each to San Nicolas and Santa Barbara Islands. The remaining 50 are distributed on two or more islands, with 20 in the Southern Channel Islands (many also on Guadalupe), 13 in the Northern Channel Islands, and 17 in both groups. A dozen or more maritime species or subspecies are nearly restricted to the islands but still retain a foothold on the mainland of southern or Baja California. More detailed information about the endemic seed plants on the Channel Islands and Guadalupe may be found in Raven (1963, 1967) and Thorne (1967, 1969).

One might well ask why we think that these island endemics are mostly relicts and not island autochthons. For many of the endemics we must rely upon inference and rather circumstantial evidence. However, the dozen near-endemics mentioned above, most of them such distinctive plants as *Coreopsis gigantea* (Kell.) Hall, *Eriogonum grande* Greene, *Eriodictyon traskiae* Eastw., *Hemizonia greeneana* Rose, *Prunus ilicifolia* subsp. *lyonii* (Eastw.) Raven, *Salvia brandegei* Munz, and *Senecio lyonii* A. Gray, illustrate well plants that would be island endemics if their limited mainland representation should be wiped out by further desiccating change in the mainland climate or further disruptive activity by man. The limited fossil record is quite helpful in supplying fossilized remnants from interior California and Nevada of Miocene and Pliocene equivalents of such noteworthy woody island endemics or near endemics as *Ceanothus arboreus* Greene, *C. megacarpus* subsp. *insularis* (Eastw.) Raven, *Cercocarpus traskiae* Eastw., *Lyonothamnus floribundus* subsp. *asplenifolius* (Greene) Raven, *Prunus ilicifolia* subsp. *lyonii*, and *Quercus tomentella* Engelm. Several of these have related species in the uplands of southern Mexico (Axelrod, 1967a, 1967b).

There are also relict endemic species among the terrestrial vertebrates. Of the four endemic reptiles (J. M. Savage, 1967), three species endemic to Cedros Island are merely insular derivatives of mainland taxa. One endemic lizard, restricted to the outer islands of San Nicolas, Santa Barbara, and San Clemente, is, however, a primitive night lizard of the genus *Klauberina*. The three remaining related genera of the family Xantusiidae are found in arid or semi-arid southwestern North America and tropical Middle America and Cuba. A fifth genus is known from the Oligocene of Wyoming. One species of the salamander genus *Batrachoseps* is relict in a few isolated populations on Santa Cruz Island, the Monterey Peninsula, the southern Sierra Nevada, and the Sierra San Pedro Martir of Baja California. The rest of the amphibians and reptiles are vagile forms that have probably populated the islands by random over-water dispersal during late Pleistocene or Recent time.

The only endemic species of mammal on the islands is the Channel Islands fox, a diminutive gray fox, *Urocyon littoralis*, on the six largest Channel Islands. It appears to be a relict species whose closest relatives are three species of similarly small, gray foxes of Yucatan, Mexico, and Guatemala. These all appear, according to Bloeker (1967), to be more closely related to each other than any of them is to the common mainland gray fox, *Urocyon cinereo-argenteus*. Two of the most distinctive endemic mammals of the islands are known only from the late Pleistocene fossil record, the giant mouse, *Peromyscus nesodytes*, of the northern Channel Islands and the dwarf mammoth, *Mammuthus exilis*, of the Northern Channel Islands and San Nicolas. This last species was apparently hunted to extinction by the early aboriginal inhabitants of the northern islands. It is the one organism known from the California Islands that would seem to require former land connections to the mainland and between the islands it occupied.

AUTOCHTHONOUS ENDEMISM

The California Islands, like most fringing archipelagos, function primarily as refugia for relicts rather than as evolutionary factories. They can in no way match such centers of evolution as the oceanic Hawaiian and Galapagean archipelagos. None the less, there has been some evolution on the islands. The deer mouse, *Peromyscus maniculatus*, is the most widely distributed and abundant mammal on 12 of the Channel Islands. It has radiated mildly into eight insular subspecies that occupy every habitat from the sandy beaches and rocky cliffs to the highest mountain tops (Bloeker, 1967). The island fox, *Urocyon littoralis*, has formed races on the six largest Channel Islands. The adorned shrew, *Sorex ornatus*, and California ground squirrel, *Spermophilus beecheyi*, have each developed a geographic race on Santa Catalina distinct from the mainland races. The big-eared harvest mouse, *Reithrodontomys megalotis*, has developed insular subspecies on Santa Catalina and Santa Cruz; and the spotted skunk, *Spilogale gracilis*, has evolved an insular subspecies on Santa Cruz and Santa Rosa. The Santa Cruz jay seems to be the one bird on the Channel Islands that may have differentiated subspecifically on the islands (T. R. Howell, 1967). The amphibians and reptiles perhaps evolve more slowly, for no subspeciation on the Channel Islands is mentioned by J. M. Savage (1967).

Autochthonous evolution on the islands is somewhat harder to prove among the seed plants. Carlquist (1965) has submitted a good probable example of adaptive radiation by flowering plants on the California Islands with his discussion of the shrubby tarweeds of the section *Zonamra* of the genus *Hemizonia* DC., whose species are largely restricted to these islands. Aside from the one fully mainland species, *H. minthornii* Jeps. of the Santa Susanna Mountains of Los Angeles and Ventura Counties, and colonies of *H. greeneana* Rose (recently described as subsp. *peninsularis* Moran, 1969) on Todos Santos and the coast of Baja California, the species are distributed over the islands, with *H. clementina* Brandegee on five of the Channel Islands, *H. streetsii* A. Gray on the San Benitos, and *H. frutescens* A. Gray in S. Wats., *H. greeneana* subsp. *greeneana*, and *H. palmeri* Rose on Guadalupe. Possibly, however, these five species did not evolve on the

islands, as suggested by the remnant populations of *H. greeneana* subsp. *peninsularis* on the Baja California coast. At least three of the island populations of *H. clementina*, however, show differences in leaves and vesture that suggest incipient subspeciation.

The genus *Dudleya* of the Crassulaceae may offer another example of radiation on the islands. Aside from eight species on the onshore islands of Baja California, there are at least nine species distributed on Guadalupe and the southern California Islands (Moran, 1959). *Dudleya blochmanae* subsp. *insularis* Moran, *D. candelabrum* Rose, *D. greenei* Rose, *D. guadalupensis* Moran, *D. hassei* (Rose) Moran, *D. traskiae* (Rose) Moran, and *D. nesiotica* Moran are restricted to the islands. *Dudleya virens* (Rose) Moran of Santa Catalina, San Clemente, and Guadalupe Islands has also one station on coastal bluffs at Point San Vicente of the Palos Verdes Hills, a former island. *Dudleya caespitosa* (Haw.) Br. & Rose is found on the Anacapa Islands as well as on the sea bluffs of the mainland from Monterey to Los Angeles Counties. Some of these species may well have differentiated on insular sea bluffs while others evolved on mainland sea bluffs. If *D. hassei* of Santa Catalina ever occurred on the mainland, it is surprising that it is not still here. At least at the Rancho Santa Ana Botanic Garden, Claremont, it is our most successful species of *Dudleya*, almost weedy in its aggressiveness. Aggressiveness certainly is not a characteristic usually associated with island endemics.

Another genus well developed on the islands is *Lavatera* L., the tree mallows of the Malvaceae. There are four California species, all insular. *Lavatera assurgentiflora* Kell. of the Channel Islands is most variable, each insular population appearing rather distinct and suggesting incipient subspeciation, as was the case in *Hemizonia clementina*. *Lavatera venosa* S. Wats. is restricted to San Gerónimo and San Benito Islands and rocks near the mouth of San Bartolomé Bay of Baja California (Moran & Lindsay, 1951). *Lavatera occidentalis* S. Wats. occurs on Los Coronados and Guadalupe and *L. lindsayi* Moran only on Outer Islet, with *L. occidentalis*, off Guadalupe. The susceptibility of these succulent-leaved plants to grazing animals, as illustrated on Santa Catalina where they now can be found only on the small islets of Indian and Bird Rocks, and on Guadalupe where they are also restricted to Outer Islet or inaccessible cliffs of the main island, may account for their almost total absence from the mainland. Presently *L. assurgentiflora*, along with the introduced Mediterranean species *L. arborea* L. and *L. cretica* L., is established along the mainland coast, especially in central and northern California.

The wild-tomato of the islands, *Solanum wallacei* (A. Gray) Parish, is probably derived from common ancestry with the mainland *S. xanti* A. Gray. It seems to have developed distinct subspecies on Guadalupe, on Santa Catalina, and on Santa Rosa and Santa Cruz Islands. *Solanum wallacei* subsp. *wallacei* of Santa Catalina has viscid, tawny-villous leaves, large purplish-blue corollas (2–4 cm broad), and dark purple berries 1.5–2.5 cm thick. *Solanum wallacei* subsp. *clokeyi* (Munz) Thorne of the Northern Channel Islands has less tawny and viscid foliage, smaller corollas (1.5–2 cm wide), and yellow berries 1–1.5 cm thick. The unnamed Guadalupe subspecies has leaves and flowers much like those on

Santa Catalina but smaller, yellow to plum-colored fruit like those of *S. wallacei* subsp. *clokeyi*.

Eriogonum giganteum S. Wats., the giant wild buckwheat of the Southern Channel Islands, though apparently a relict species, seems to have differentiated into three subspecies with *E. giganteum* subsp. *giganteum* on Santa Catalina, *E. giganteum* subsp. *formosum* (K. Brandgee) Raven on San Clemente, and *E. giganteum* var. *compactum* Dunkle on Santa Barbara Island. Subspeciation seems to have occurred also in another relict, *Lyonothamnus floribundus* A. Gray. *Lyonothamnus floribundus* subsp. *floribundus*, with entire leaves, is known only from Santa Catalina. *Lyonothamnus floribundus* subsp. *asplenifolius* with pinnate-pinnatifid leaves, not found on Santa Catalina, is found to the south on San Clemente, to the north on Santa Cruz and Santa Rosa Islands, and extensively in the Miocene and Pliocene fossil record of mainland California and Nevada. *Lyonothamnus floribundus* subsp. *floribundus* is apparently unknown as a fossil. It seems to be a recent development and not a major genetic modification. The juvenile leaves are pinnate like those of the other subspecies, and injured or otherwise disturbed trees and branches produce pinnatifid or partially pinnate leaves intermediate between the leaves of the two subspecies.

Other taxa on the islands that show infraspecific or even specific insular differentiation are *Arctostaphylos* (see Wells, 1968), *Brodiaea* Sm. (*sens. lat.*), *Camissonia guadalupensis* (S. Wats.) Raven, *Delphinium* L., *Eschscholzia* Cham., *Galium* L., *Lotus argophyllus* (A. Gray) Greene, *L. scoparius* (Nutt. in T. & G.) Ottery, *Malacothrix* DC., and *Mimulus* L.

INSULAR GIGANTISM

The tendency on oceanic islands toward prolonged growth, woodiness, and arborescence in taxa that are normally herbaceous is one of the most fascinating phenomena of island life. Particularly famous examples are the arborescent lobeliads of Hawaii and southern Polynesia; woody lettuces of the Juan Fernandez, Desventuradas, and Canary Islands; other rosette-shrub or tree composites of the Juan Fernandez, St. Helena, and Galapagos Islands; and shrubby or arborescent chenopods, amaranths, and four-o'clocks of Hawaii (Carlquist, 1965). Although the California Islands have not produced such spectacular plants, they nevertheless exhibit good examples of prolonged growth and woodiness. On Santa Catalina I found one specimen of *Eriogonum giganteum* subsp. *giganteum*, depicted in my flora of the island (Thorne, 1967), that had one stem 12 feet tall with a four-foot spread and a trunk diameter of 5 inches at 3 feet above the ground. *Eriogonum arborescens* Greene is also a sizable shrub. The islands even have their own woody lettuces, with *Munzothamnus blairii* (Munz & Johnst.) Raven, depicted in Raven's San Clemente flora (1963) growing on a vertical canyon wall, and its distant cousin on Guadalupe, *Stephanomeria guadalupensis* Brandege. The *Munzothamnus* is a straggly shrub with stems to 7 cm in diameter and to 2 m long, often pendulous; the *Stephanomeria* is less massive with a stem to 3 or 4 dm high.

Insular woodiness is also well represented in other composite tribes. The shrubby *Hemizonia* tarweeds (Madiinae) of the California Islands have been dis-

cussed above. The remarkable *Coreopsis gigantea* (Heliantheae) is a rosette-shrub with tufts of much-dissected leaves borne at the ends of the stout fleshy stems up to 12 cm thick and 2 or 3 m tall. Guadalupe and the Channel Islands share it together with rocky bluffs and exposed dunes along the mainland coast from San Luis Obispo County to Los Angeles County. The Heleneae, perhaps not truly distinct from the Heliantheae, are represented by *Eriophyllum nevinii* A. Gray, a handsome shrub with leaves white-tomentose on both sides, of the Southern Channel Islands, and by *Perityle incana* A. Gray of Guadalupe Island. *Haplopappus canus* (A. Gray) Blake of Guadalupe and San Clemente and *H. detonsus* (Greene) Raven of the Northern Channel Islands belong to the Astereae; and *Senecio palmeri* A. Gray of Guadalupe and *S. lyonii* A. Gray of Santa Catalina and San Clemente, and of San Martin and adjacent Bahia de San Quintin of Baja California, to the Senecioneae.

Woodiness on the islands is by no means restricted to the Polygonaceae and Asteraceae. In the Papaveraceae, in addition to the expectedly woody *Dendromecon rigida* subsp. *rhamnoides* (Greene) Thorne and *D. rigida* subsp. *harfordii* (Kell.) Raven of the Channel Islands, there is a woody poppy or two on Guadalupe, *Eschscholzia* (*Petromecon*) *palmeri* Rose and *E. (Petromecon) frutescens* Greene. *Erysimum insulare* Greene (Brassicaceae) of Guadalupe's Outer Islet and the Northern Channel Islands and *Galium angulosum* A. Gray (Rubiaceae) of Guadalupe are woody-stemmed suffrutescent perennials. *Talinum guadalupense* Dudley (Portulacaceae) of Guadalupe is a succulent shrub with beautiful pink flowers, and *Galvesia speciosa* (Nutt.) A. Gray (Scrophulariaceae), the bush-snapdragon of Santa Catalina, San Clemente, and Guadalupe, is an arching or pendulous shrub on steep sea bluffs and canyon walls. Whether most of these unusually woody plants evolved on the islands or, more likely, under a moderate maritime climate along the mainland coasts would now be hard to determine. Several, like *Coreopsis gigantea*, *Senecio lyonii*, *Hemizonia greeneana*, and *Dendromecon rigida*, do occur on the mainland. And the shrubby *Euphorbia misera* Benth. is shared by the maritime desert scrub of the southern islands and the southern mainland and by the desert coasts of Sonora and the islands in the Gulf of California.

It may be pertinent to mention here that the harvest mouse, deer mouse, ground squirrel, and spotted skunk on the Channel Islands (Bloeker, 1967) and the Santa Cruz jay (T. R. Howell, 1967) are all larger than their mainland counterparts. The island fox is much smaller than the mainland gray fox, but, as stated above, it may be much more closely related to similarly diminutive gray foxes in Middle America. The extinct giant mouse, *Peromyscus nesodytes*, of the islands adds further weight to this apparent mild gigantism in small mammals. The extinct dwarf mammoth, *Mammuthus exilis*, of late Pleistocene time, however, was much smaller than its mainland counterpart, the imperial elephant, *Mammuthus imperator*. It calls to mind the extinct pygmy hippopotamus that was abundant on Madagascar during Pleistocene time. It would seem that restriction of space on islands leads to diminished size or extinction of larger mammals relict on them or reaching them over water, while permitting increase in size of the smaller mammals.

CONTINUOUS FLOWERING

The continuously temperate, maritime climate that allows prolonged growth among the island herbs also favors continuous or nearly continuous flowering among several of the evergreen shrubs. The mainland subspecies of tree poppy, *Dendromecon rigida* subsp. *rigida*, has a relatively brief flowering period, but the island subspecies, *D. rigida* subsp. *rhamoides* and *D. rigida* subsp. *harfordii*, seem to bloom almost continuously. This has been observed both among wild plants and among our plantings of mainland and island subspecies at the Rancho Santa Ana Botanic Garden. The bush-snapdragon, *Galvesia speciosa*, blooms continuously in our Garden also, as it presumably does on its island homes. *Lavatera assurgentiflora* and *Crossosoma californicum* have long blooming periods in the Garden, and perhaps many other less conspicuous island plants would prove, upon careful observation, to have similarly prolonged flowering.

HYBRIDIZATION

The ability of island plants to hybridize freely has often been noted. Certainly the plants of the California Islands are no exception. One wonders why the island habitat leads to such promiscuity among the plants. There is surely some selective advantage from the increased variability brought into island populations by gene introgression (Carlquist, 1966). The oaks of Guadalupe and the Channel Islands are perhaps the most notorious hybridizers. *Quercus* × *macdonaldii* Green, a rather frequent, large, spreading tree on Santa Catalina, is apparently the hybrid offspring of *Q. dumosa* Nutt. and *Q. lobata* Neé. Less conspicuous but abundant are the apparent backcrosses with both putative parent species. Trees of *Quercus chrysolepis* Liebm. on Mt. Orizaba, Santa Catalina, seem to show varying degrees of heavy to light introgression from nearby groves of the island oak, *Q. tomentella* Engelm. The extraordinary variability of the scrub oak, *Q. dumosa* Nutt., on the Channel Islands must in part derive from introgression from other species, especially from *Q. lobata* and less commonly from *Q. engelmanni* Greene and *Q. douglasii* H. & A. (Muller, 1967).

Hybridization is even more extreme among the native low-spreading or prostrate prickly-pears that abound over most of the Channel Islands. Hybridization among them and with the introduced mission cactus, *Opuntia ficus-indica* (L.) Mill., is so rampant and the variation pattern so complex that it is nearly impossible to identify most of the plants seen. The two primary indigenous species involved are *O. littoralis* (Engelm.) Cockerell var. *littoralis* and *O. oricola* Philbrick, though other species, as *O. phaeacantha* var. *discata* (Griffiths) Bens. & Walk. and "*O. demissa* Griffiths," may also be participating.

Other genera also seem to hybridize freely on Santa Catalina. Apparent hybrids between the evergreen sumacs *Rhus ovata* S. Wats. and *R. integrifolia* (Nutt.) Benth. & Hook. ex Rothr. seem to be rather frequent as do also those between *Dudleya virens* and *D. hassei*. Less frequent are the apparent hybrids between *Salvia apiana* Jeps. and *S. mellifera* Greene. At the one station found on Santa Catalina for the rare island endemic rock-rose *Helianthemum greenei* Robins. (Cistaceae) the more common *H. scoparium* Nutt. var. *vulgare* Jeps. was also

found with an apparent hybrid intermediate in appearance between the two putative parent species. Likewise at the only station for the nearly extinct and striking Catalina-mahogany, *Cercocarpus traskiae* Eastw. (Rosaceae), in a canyon on the Salta Verde, Santa Catalina, one or two of the few remaining trees appear to show genic introgression with *C. betuloides* var. *blancheae* (C. K. Schneid.) Little, which is also present in the canyon.

In a few instances hybridization on Santa Catalina seems to have "swamped out" one of the putative parents. I was unable to find any "pure" specimens of *Quercus lobata* despite the apparent abundance of hybrid offspring between it and *Q. dumosa*. *Q. chrysolepis* on Santa Catalina may in a few more generations be swallowed up genetically by *Q. tomentella*. *Cercocarpus traskiae* may similarly disappear into *C. betuloides* var. *blancheae*. The populations of *Ceanothus megacarpus* Nutt. (Rhamnaceae) on both San Clemente and Santa Catalina seem to represent a hybrid swarm between the mainland subsp. *megacarpus* and the insular subsp. *insularis* (Eastw.) Raven. The leaves resemble the latter more closely in size but are mostly alternate as in the former. The capsules vary from the conspicuously horned *megacarpus* types to the almost hornless *insularis* types. The bush monkey-flower, *Mimulus (Diplacus) puniceus* (Nutt.) Steud. (Scrophulariaceae) on Santa Catalina represents, according to McMinn (1951), "hybrid swarms which have probably resulted from the crossing and back-crossing" of *M. puniceus* with *M. longiflorus* (Nutt.) Grant. "Pure" *M. longiflorus* seems to have been "swamped out" by *M. puniceus*, for I could find no traces of it among the numerous and varied representatives of the bush monkey-flower on the island. Apparent hybrids between *M. longiflorus* and *M. flemingii* Munz are frequent on Santa Cruz Island with the putative parents.

In all fairness to mainland hybridization, one must admit that *Quercus*, *Opuntia*, *Diplacus*, *Salvia*, *Rhus*, *Dudleya*, *Ceanothus*, and other genera appear to be pretty promiscuous on the mainland also, though I have never observed the prevalence of hybridization in mainland populations that I have found in insular populations.

VULNERABILITY

A most unfortunate characteristic of insular plants and animals is their vulnerability. Under insular conditions there is usually rather complete protection from large predators and from large grazing animals. The waif origin of the biota leads to many open niches and a relatively low level of competition among the species present. This general freedom from the predators, grazers, browsers, and competitors that abound on adjacent continental land masses places no great selective value on the usual defences "built-in" to the genotypes of mainland plants and animals. The instinctive or "learned" wariness of animals on the mainland is often replaced on islands by a fearlessness that makes the animals ready prey for introduced mainland predators. The lack of timidity of the small island foxes on Santa Cruz, which stood unafraid and watched us with apparent curiosity and which are reputed to feed from the hands of visitors to the biological laboratory there, is one example of this phenomenon. Another is the indifference to man of the northern elephant seals, *Mirounga angustirostris*, on their hauling-out beaches

on the islands. Even the common green rattlesnake, *Crotalus viridis*, on Santa Catalina seemed quite unaggressive and usually rather indifferent to man, though I did not venture to handle it during several encounters on the island.

When predators like man, feral cats, and dogs are introduced to an island, the depredation on the animal life is rapid and often complete. The disappearance of the pigmy mammoth from the Northern Channel Islands is rather surely the work of aboriginal man. The commercial sealers of the early nineteenth century all but exterminated the northern elephant seal and the Guadalupe fur seal, *Arctocephalus phillippii townsendi*. Both have fortunately made phenomenal come-backs since they became legally protected by the Mexican and American governments in the early twentieth century. The sea otter, *Enhydra lutris*, was exterminated in the southern California islands by the fur-hunters, though a pitiful remnant did survive in the Monterey region. Now the protected California coastal population is increasing, and occasional stray otters are seen among the Northern Channel Islands. On many of the islands some or all species of ground-nesting bird have been exterminated by feral cats. The elimination of most of the endemic birds of Guadalupe Island has been attributed to such predators (Moran & Lindsay, 1950).

The devastation of the island floras by the white man and his introduced goats, sheep, and pigs has been pathetic. We can only surmise what the vegetation and floras must have been like before the advent of goats and sheep on Guadalupe, San Clemente, San Nicolas, parts of Santa Catalina, and the other islands. On Guadalupe numerous species have been eliminated. The monotypic genus *Hesperelaea* is apparently extinct, presumably cut for a goat corral (Brandege, 1900). The groves of *Juniperus californica* Carr. reported by Palmer (*in* Watson, 1876) are gone. The species is presently represented by a few scraggly individuals (Moran, personal communication, 1970). No reproduction of the other tree species, as *Cupressus guadalupensis* S. Wats., *Pinus radiata* Don, *Erythea edulis* (Wendl.) S. Wats., and *Quercus tomentella*, is permitted by the goats. On Guadalupe these species seem to be doomed with the passing of the present generation of trees. Five species of the plants found on goat-free Outer Islet (Moran, 1967, 1969) two miles south of the main island, have never been found on the main island, though they were surely once there. The species of *Lavatera* mentioned above are prime examples of vulnerable plants (Brandege, 1900) that can survive only on inaccessible cliffs or on goat-free rocks off the main islands.

After much intensive collecting on Santa Catalina by many botanists for many years, we have been unable in the last 25 or 30 years to recollect 43 (of 396) indigenous species found on the island by earlier botanists. Some of these plants, as is also true on the other islands, have not been seen since they were collected by the first botanists to visit the island. The succulent grass *Dissanthelium californicum* (Nutt.) Benth., reported by Palmer as most attractive to the goats, was collected just once each on Guadalupe, San Clemente, and Santa Catalina. It has presumably been eliminated by these voracious herbivores. Perhaps ten or more of the endemic flowering plants described from the California Islands have already been exterminated.

LOSS OF DISPERSIBILITY

Loss of dispersibility, characteristic in plants and animals on oceanic islands (Carlquist, 1965), is not expected among the biota of a fringing archipelago. Because of recent connections with the mainland or the relative ease of dispersal of plant and animal species to islands close to continental areas, there usually has been too little time for evolution by the island inhabitants toward loss of flight among birds and insects or increased seed size among the plants. Furthermore, the presumed constant influx of continental waifs may quickly "swamp out" or eliminate through competition the less aggressive populations of the same or related species or unrelated species occupying the same ecological niches. Thus, one would expect to find loss of dispersibility only, if at all, on the most ancient and isolated of the California Islands, Guadalupe. On Guadalupe there is one likely candidate that has suffered a loss of dispersibility for over water dispersal at least, through enlargement of its edible fruit. The Guadalupe palm, *Erythea edulis*, has a black, globose drupe that is 25–35 mm in diameter with soft pulp and a nutlet about 20 mm in diameter crosswise (Bailey, 1937). The closest relative geographically is the blue palm, *E. armata* S. Wats. of Baja California with fruits (11–) 18–24 mm long and nutlets usually about 15 mm in diameter. The closest species morphologically is *E. aculeata* Brandegee, the Sinaloa palm, with fruits 20–25 (–28) mm long and nutlets about 15 mm across. The other three mainland Mexican species also have smaller fruits and smaller, often thinner nutlets than *E. edulis*. T. R. Howell (1967) suggested that the now extinct Guadalupe caracara, *Polyborus lutosus*, might have fed on palm fruits and brought mainland seed to the island. I do not know whether ravens have ever formed part of the avifauna of Guadalupe, but about Santa Catalina Island they are most active and playful carriers of large fruits.

EPILOGUE

Should any of the readers of this paper wish to avail themselves of these insular refugia and laboratories of evolution, they might appreciate some information about available facilities on the islands and institutions or persons to approach. The University of California, Santa Barbara, now has a permanent field station on Santa Cruz Island. One can obtain information about the use of facilities there by writing to the Department of Biology, University of California, Santa Barbara, Goleta, California 93017. Similarly the University of Southern California has constructed a marine laboratory, the Marine Science Center, at the Isthmus on Santa Catalina Island. Since most of the island is owned by the Santa Catalina Island Company, Avalon, permission to collect and travel about the island should be sought from the Company. Mr. Douglas Propst, Ranch Superintendent for the Company, is an informed and enthusiastic naturalist and conservationist and has been most helpful to various scientists with projects requiring field study on the island.

The National Park Service, through its Channel Islands National Monument, has jurisdiction over Santa Barbara, San Miguel, and the Anacapa Islands. For information about visits to and studies on these islands one should get in touch

with the Chief Scientist, Channel Islands National Monument, Port Hueneme, California. To obtain permission to visit and travel about San Clemente Island, one should write to the Commanding Officer, United States Naval Ordnance Test Station, Pasadena Annex, California. San Nicolas is also under the jurisdiction of the United States Navy Department, Pacific Missile Range, Point Mugu, California 93041. Santa Rosa Island is privately owned, and permission to do scientific work there would have to be obtained from the owner, Mr. Al Vail.

The Baja California Islands belong to the Mexican Government and are less easy to visit. I can offer no helpful information about field work on them except to mention that Dr. Reid Moran, Curator of the Department of Botany, San Diego Natural History Museum, is the outstanding authority on their flora.

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